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Testing Darwin's transoceanic dispersal hypothesis for the inland nettle family (Urticaceae)

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in the paper and to revisions.

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1 **Abstract**

2 Dispersal is a fundamental ecological process, yet demonstrating the occurrence and
3 importance of long-distance dispersal (LDD) remains difficult, having rarely been
4 examined for widespread, non-coastal plant groups. Therefore, we integrated
5 phylogenetic, molecular-dating, biogeographical, ecological, seed biology, and
6 oceanographic data for the cosmopolitan, primarily inland Urticaceae. We found that
7 Urticaceae originated in Eurasia ~69 Ma, followed by ≥ 92 LDD events between
8 landmasses. Under experimental conditions, seeds of many Urticaceae floated for >220
9 days, and remained viable after ten months in seawater, long enough for most detected
10 LDD events, according to oceanographic current modeling. Ecological traits analyses
11 indicated that preferences for disturbed habitats might facilitate LDD. Nearly half of all
12 LDD events involved dioecious taxa, so population establishment in dioecious
13 Urticaceae requires either multiple seeds, or occasional selfing. Our work shows that
14 seawater LDD might be a valid mode of transportation for inland plants, providing
15 empirical evidence for Darwin's transoceanic dispersal hypothesis.

(a) Introduction

Dispersal is a central biogeographical process shaping the present-day distributions of organisms (Lomolino *et al.* 2010; Saastamoinen *et al.* 2018). For sessile organisms such as plants, dispersal occurs via the movement of propagules or gametes (e.g. through spores, seeds and pollen) away from parents (Clobert *et al.* 2001; Petit 2004); this, along with environmental conditions and species interactions, determines when and where species are found.

Darwin (1856) was an early advocate of the importance of dispersal, and he demonstrated that many plant seeds could survive more than one month's immersion in saltwater, thus potentially facilitating migration between landmasses, although he felt that sinking might be an issue. For the next hundred years, long-distance dispersal (LDD) was implicated as the cause of many present-day disjunctions across ocean barriers, although successful LDD has been rarely witnessed (Nathan 2006). However, during the 1960-70s, the validation of plate-tectonic theory and the spread of cladistic thinking drastically reduced the perceived importance of oceanic LDD, providing instead an attractive vicariant explanation for plant disjunctions (de Queiroz 2005; Cowie & Holland 2006; Milne 2006). Consequently, for a time, LDD largely fell out of favor, being regarded as unfalsifiable and even unscientific (Nelson 1978).

The advent of molecular dating, combining molecular phylogenetics with fossil calibration, however, repeatedly revealed cases of transoceanic disjunctions that were too young to result from tectonic vicariance (Givnish *et al.* 2004; Popp *et al.* 2011; Bourguignon *et al.* 2018; Guo *et al.* 2018), forcing the scientific community to accept

other explanations for disjunctions, leading to increasing acceptance of the role of LDD in shaping the present distributions of organisms (Raxworthy *et al.* 2002; Pyron 2014; Rota *et al.* 2016; Carlton *et al.* 2017; Luebert *et al.* 2017). LDD events are now universally accepted as a major factor shaping global biogeography, including large-scale processes such as population spread, biodiversity evolution of oceanic islands, and colonization of unoccupied habitats (Levin *et al.* 2003; Trakhtenbrot *et al.* 2005; Cowie & Holland 2006; Gillespie *et al.* 2012).

Regarding mechanism, oceanic LDD has been reevaluated and is now hypothesized as the main cause of disjunct distributions in many groups (Samonds *et al.* 2012; Wee *et al.* 2014; Correia *et al.* 2018). Nonetheless, it remains difficult to demonstrate experimentally or from observations how LDD occurred in any particular case, largely because of the rarity and presumed unpredictability of such events (Gillespie *et al.* 2012). Therefore, it is important that LDD hypotheses should be testable using independent lines of evidence (Crisp *et al.* 2011).

Ocean currents have repeatedly been shown to be very important to LDD (Harwell & Orth 2002; Thiel & Haye 2006; Geng *et al.* 2008; McMahon *et al.* 2014; Smith *et al.* 2018). However, most such studies concern relatively recent (post-Pliocene) LDD events, focus on littoral species that often have specific adaptations to seawater dispersal, concern groups with a relatively limited geological range, and/or rely either on phylogeography or anecdotal observations alone (Table S1). Where widely distributed inland groups have been examined, phylogenetic reconstruction has normally been the focus, and LDD has only been hypothesized from this evidence

without direct investigation into possible mechanisms for it (Mao *et al.* 2010; Boer *et al.* 2015; Cano *et al.* 2018; Yang *et al.* 2018).

LDD of plant propagules across oceans can occur by transportation through air (wind or birds) or on ocean currents through immersion in seawater or on floating vegetation islands (Nathan *et al.* 2008). To make a strong case for the oceanic transport of propagules, for a given plant group, requires three lines of evidence. First, LDD needs to be implicated as a potential explanation for the disjunct distribution of populations within species or sister taxa on different landmasses, which in turn requires precise molecular phylogenetic reconstruction. Second, ocean currents must be shown to be the most likely mechanism of LDD. Third, the ability of seeds to make long journeys in ocean currents must be demonstrated, using taxa descended from those determined to have undergone LDD.

The nettle family (Urticaceae) constitutes an ideal group for examining LDD, because it has a worldwide distribution, and a recent phylogeny revealed many intercontinental disjunctions, indicating many probable LDD events (Wu *et al.* 2013). Moreover, individual Urticaceous plants produce large numbers of seeds, and these seeds are dispersed in tiny and hard achenes, mostly <10 mm and often <1 mm across, that have no obvious adaptations to long dispersal by animals or wind. Most species occur in wet understory environments along watercourses (Chen *et al.* 2003) where exposure to wind is limited, making LDD by air, especially wind, highly unlikely, whereas seeds could easily be carried downstream into the sea, making dispersal via seawater seem a likely mechanism for LDD in this family.

For the current study, we first reconstructed the most complete generic-level phylogeny of Urticaceae to date, and then used this as a framework to investigate the biogeography and diversification of Urticaceae in space and time, identifying likely LDD events across ocean barriers. Second, we selected four important ecological traits that might be associated with particular modes of dispersal, and mapped these onto our phylogeny in order to test whether each trait was more common in nodes where LDD occurred than across the whole tree, which would imply that it promoted dispersal, hence providing clues to likely mechanisms. Third, we conducted a rigorous examination of seed biology to determine the buoyancy and viability of seeds after long-term exposure to seawater, and combined this with oceanographic current modeling to determine how far seed could be expected to travel in seawater. From this, we examined the frequency, routes and mechanisms of LDD across Urticaceae.

(b) Materials and Methods

Taxon sampling and phylogenetic analyses

We sampled 298 accessions of 258 species from 52 genera of Urticaceae, representing 94.5% of the recognized genera, and covering the entire geographical range of the family. As outgroups, we used 26 species representing 14 genera from the 3 most related families (Moraceae, Cannabaceae, and Ulmaceae) in the Rosales. In total, we sampled 325 accessions (Appendix S1, Table S2), and examined seven loci from three genomes, comprising four chloroplast genes or intergenic regions (*trnL-trnF*,

rpl4-rps8-infA-rpl36, *matK* and *rbcL*), two nuclear regions (ITS and 18S), and one mitochondrial gene (*matR*). The total aligned length was 11973 bp. DNA isolation, PCR amplification, sequencing, and phylogenetic analysis all followed Wu *et al.* (2013) (Table S3, Appendix S1).

Divergence time estimation

We estimated a time-calibrated phylogeny using the Bayesian program BEAST v 1.7.5 (Drummond *et al.* 2012), and the four most reliable Urticaceae fossils plus one outgroup fossil were used as calibration points to determine absolute age of divergence (Appendix S2).

Ancestral area reconstruction and diversification analyses

To determine the historical biogeography of Urticaceae, two distinct but widely used methods of inferring biogeographic histories were employed: The dispersal-extinction-cladogenesis (DEC) model was implemented in the software LAGRANGE (Ree & Smith 2008), and S-DIVA (Yu *et al.* 2010) was implemented in RASP 3.2 (Yu *et al.* 2015) (Table S4, Appendix S2).

To explore the tempo and mode of species diversification rates in Urticaceae over time, we performed diversification analyses in the R package using the *ape* library (Paradis *et al.* 2004) (Appendix S2).

Evolutionary trends, correlations to LDD, correlated evolution and phylogenetic signal in ecological traits

Evolutionary trends- Dispersal tends to covary with a number of morphological, ecological and behavioral traits (Stevens *et al.* 2014), hence such traits have a likely impact on the feasibility of different modes of LDD. Hence we selected four important ecological traits (sexual system, epiphytic life style, wet/dry habitat, and degree of habitat disturbance) that might be associated with particular modes of dispersal, and mapped them onto our phylogeny (Appendix S3). Ancestral states were reconstructed for all such characters using the maximum likelihood (ML) method, following Wu *et al.* (2015) (Table S5).

Correlations to LDD- For the definition of LDD in this study see Appendix S3. For each trait, the likely state was determined for every node and terminal, giving an average value across the tree; this was then compared to the mean value across only those nodes associated with a detected LDD event.

Correlated evolution - To test the correlation among all four of these characters for statistical validity, we employed Maximum likelihood (ML) and Markov chain Monte Carlo (MCMC), using for both the discrete model conducted in BayesTraits v 1.0 (Appendix S3).

Phylogenetic signal test - a) To test whether presence/absence of LDD events are distributed randomly across the phylogeny, we used the *phylo.d* function in the caper package in R (Fritz & Purvis 2010). The value of D can be both smaller than 0 (highly conserved) and greater than 1 (over-dispersed). b) We determined whether sexual

system, epiphytic life style, wet/dry habitat, and degree of habitat disturbance exhibited phylogenetic signals. The first three were binary variables, and were also tested using the function *phylo.d*. For habitat disturbance there were three possible states (Appendix S3), so we firstly calculated the observed parsimony score (number of character changes along the tree), then the null expectations were generated from the randomizations of 999 times the habitat disturbance across the species. The standardized effect size (SES) was calculated by subtracting the observed parsimony score from the mean parsimony score from null randomizations and dividing by the standard deviation of the randomized score (Maddison & Slatkin 1991).

Saltwater immersion tolerance test for seeds

To investigate whether seeds of Urticaceae can remain viable when immersed in salt water, we carried out rigorous immersion experiments. Throughout this paper, “seeds” refers to achenes, which is the form in which they are released in all Urticaceae.

Firstly, based on our biogeographic results, we identified 12 species (Table S6) that had unequivocal intercontinental LDD events in their ancestry, representing all of the four major subfamily-level clades (Clades I-IV) comprising the family (Fig. S1). Seeds of each species were placed in plastic Petri dishes (90 mm diameter) with NaCl solutions of concentrations below (0%, 1%), equal to (3.5%; Sverdrup *et al.* 1942) and above (5%, 8%) that of seawater. Solutions were renewed every month. All dishes were placed in a room with temperature at 18-25°C in the day and 10-15°C at night.

For each species, seeds were left in the NaCl solutions for each of one, three, five,

six, seven, eight, nine and ten months. After that, the seed germination of each species from each combination of concentration and time period was determined, for details see Appendix S3. An increase in salinity stress can induce physiological secondary dormancy, delaying germination (Baskin & Baskin 1998); therefore, seeds that did not germinate in our experiment might still be viable. Tetrazolium testing, a widely used alternative means of testing for seed physiological quality (Lamarca & Barbedo 2014; Oliveira *et al.* 2016), was therefore employed (Appendix S3).

From each replicate, viability percentage (VP) was calculated as total number of seeds that germinated, plus estimated number alive by Tetrazolium testing, divided by the total (excluding empty or infected seeds). A mean was then calculated for each species, time and concentration.

The effect of immersion time and NaCl concentration on VP was evaluated using Univariate General Linear Models performed using the SPSS 16.0 software package (Chicago, IL, USA). The percentage data were arcsine transformed before analysis. Differences obtained at a level of $p < 0.05$ were considered to be significant.

Additionally, to test whether 50% viability and maximum life span of the seeds from these 12 species showed a significant phylogenetic signal, we calculated the maximum likelihood value of Pagel's (1999) lambda (λ) using the functions 'fit discrete' in the *Geiger* package with 50% viability and maximum life span as a discrete character.

Seed buoyancy and LDD potential over water

Successful LDD across water requires long-term seed buoyancy as well as survival, and

we assessed buoyancy for 21 species (those 12 tested for saltwater immersion tolerance, plus nine others) (Table S7). A total of 270 seeds were taken from each species, then following Lopez (2001), these were divided evenly among six glass bottles (250 mL), of which three contained fresh water (0% NaCl) and three had 3.5% NaCl, mimicking seawater. Conditions were otherwise the same as for the saltwater immersion tolerance test. The number of floating seeds was counted at 5-day intervals.

For each species, mean seed mass (m) was determined by weighing 1000 seeds using a precision electronic balance reading up to 0.0001 g (Table S8). Seed volume could not reliably be determined using the liquid displacement method because of high buoyancy. Therefore volume (v) per seed was calculated by measuring major (L_1), intermediate (L_2) and minor (L_3) diameters from five randomly selected seeds of each species, using a Vernier caliper (to 0.01 mm), and the equation $v = \pi (L_1 L_2 L_3) / 6$ (Miller 1987); Typical seed density (ρ) for each species was then calculated according to $\rho = m/v$ (Table S8).

Two separate mechanisms underlie all seed floatation, these are air trapped between the cotyledons, and a spongy mesocarp or cork-like pericarp (van der Pijl 1972). We used a Faxitron MX-20-DC12 X-ray image system (Faxitron X-ray Corporation, Lincolnshire, IL, USA) to examine internal seed anatomy for these 21 species.

Finally, to observe the impact on the seed coat from prolonged salt water immersion, the external morphology of achenes from those species subjected to eight months immersion were compared to seeds from before immersion using a Sigma 300 scanning electron microscope.

To predict the time required for seeds to disperse from the source landmass to the destination landmass, ocean circulation models (Van Sebille *et al.* 2012; van Sebille 2014) were employed. Based on our biogeographic results, we selected eight species or small clades within which unequivocal LDD events were detected (Table S9). In each case, to set the starting point for dispersal, we first conflated the existing distributions of all species within the source clade, and then selected the closest point within this range to the destination landmass (Table S9). Next, in each case, results from ocean modeling data were combined with seed survival and flotation data, to examine the likelihood of seeds reaching the destination landmass via seawater.

(c) Results

Relationships and molecular dating

Our phylogenetic topology was consistent with Wu *et al.* (2013), strongly supporting the monophyly of Urticaceae and that of all four main Clades (Fig. S1, Appendix S4). Further, our analyses suggested that Urticaceae originated in Eurasia (56.2- 68.7 (-87.1) Ma (range indicates 95% highest probability densities; Fig. 1; Table S10).

Ancestral area reconstruction and diversification

Lagrange (Fig. 1) and S-DIVA (Fig. S2) analyses gave similar results for all nodes, but the former gives more accurate reconstructions that are better aligned with palaeogeographical evidence (Buerki *et al.* 2011), hence we describe the results here

entirely based on Lagrange.

Urticaceae arose and began to diversify within Eurasia, and a total of 92 LDD events are indicated (Fig. 1; Table 1; Appendix S5). Detailed biogeographical descriptions for all main clades of Urticaceae are provided in Appendix S4. A plot of the cumulative number of lineages through time (LTT plot) for Urticaceae indicates diversification perhaps accelerating around 45 Ma (Fig. S3, Appendix S4).

Evolutionary trends of ecological traits and their correlations to LDD

The ancestor of Urticaceae was dioecious, non-epiphytic and occupied dry habitats (Fig S4). Within Urticaceae, 45.02% of nodes and terminals were monoecious, whereas 1.01% were epiphytic and 46.04% occupied wet habitats. The respective percentages for these traits across only those nodes associated with LDD events were 51.65%, 3.30%, and 36.26%, but the differences were non-significant (see Appendix S4 for details).

Regarding level of disturbance, 9.99% of nodes and terminals occupied undisturbed habitats, 77.95% were semi-disturbed, and were 12.06% completely disturbed. Scoring 0, 1 and 2 for these states respectively, the mean value across the tree was 0.979 as opposed to 1.143 for nodes with LDD events ($t=3.740$; $p=0.00028$; Appendix S4) indicating that the likelihood of LDD increases as the preferred habitat becomes more disturbed.

Furthermore, we determined that LDD events were strongly phylogenetically conserved ($D = -0.007$, $p < 0.001$), indicating that closely related species were likely to

be ecologically similar to one another (Appendix S4).

Using ML and MCMC analysis methods, very strong support was detected for correlated evolution between habitat (wet/dry) and two other traits: sexual system ($p=0.00002$; LBF = 24.85), and completely disturbed habitat ($p=0.00023$; LBF = 8.78) (table S11).

Effect of salt concentration and immersion time on seed survival

Across all species, seed viability declined significantly as both immersion time and salt concentration increased (Fig. 2, S5 & S6, Table S12 & S13). At salt water concentration (3.5%), seeds of *Droguetia*, *Dendrocnide*, *Gonostegia*, *Maoutia* and *Poikilospermum* survived until the seed supply ran out, lasting respectively 300, 240, 270, 240, and 240 days; however, seeds of *Urtica*, *Pilea*, *Parietaria* and *Debregeasia*, survived only until 240, 210, 240, and 210 days, respectively. Similar results were observed at 1% concentration. However, seeds of *Boehmeria* and *Elatostema* were all dead after 180 days' immersion, at any concentration. Increased salt concentrations caused a decline in viability for most species after 150 days (though not *Urtica*), and only five genera showed any viability after 210 days at 8% (Table S13). There was no phylogenetic signal detected for 50% viability and maximum life span (Table S14).

Seed floatation

Germinated seed will not survive a long journey in seawater, so these are treated

as having sunk or died. In distilled water, no germination was observed in 7 species after 150 days' immersion, but 6 of the 21 species exhibited some germination from ten days on (Fig. S7; Appendix S4). Regarding flotation, 12 species had at least 60% of seeds still floating by the end, but five species had all seed sunk within 30 days (Fig. S7).

In saltwater, no germination was observed for any species, and in general more seeds remained buoyant than in fresh water (Fig. 3). After 220 days, twelve species had at least 95% of seeds still floating, four had between 70% and 95% floating after 220 days, and four had <50% of their seeds floating (Fig. 3). Among most species, most seeds that were buoyant after 20 days remained so after 220 days (Fig. 3, Appendix S4).

The mean seed density for all species was less than the density of both water ($1.0 \times 10^3 \text{ kg/m}^3$) and seawater ($1.04 \times 10^3 \text{ kg/m}^3$), indicating that the seeds should be buoyant in seawater. At least 12 of the 21 species examined using X-ray images were found to possess small but obvious air-filled cavities (Fig. S8).

Examination of the external morphology of achenes demonstrated that long-term salt water immersion produces little or no change to seed volume. This implies that the seeds have excellent waterproof properties, and that neither imbibition of seawater nor significant loss of water via osmosis has occurred. Damage was only observed to the seed coat (Fig. S9) and parts not involved in seed protection, such as persistent perianth lobes (e.g. *Boehmeria penduliflora* and *Debregeasia longifolia*, 1 and 8 in Fig. S9).

Estimating the time required for LDD using ocean circulation modeling

Regarding drift patterns and minimum transit times between continents (Fig. 4,

Table S9), three of the eight species analyzed could have reached the destination landmass via seawater within six months, with *Debregeasia longifolia* needing the least time, i.e. four months to reach the Philippines from Vietnam. *Droguetia inners* subsp. *urticoides* would need 12 months to reach Tanzania from Java, whereas *Parietaria micrantha* would need 22 months to float directly from China to Australia, but there are ample islands in between, so the journey could have been made in stages (Fig. 4). It would take the MRCA of *Neraudia*+sistergroups ca. 48 months to reach Hawaii from Japan or thereabouts.

(d) Discussion

Major disjunctions in Urticaceae and identifications of oceanic dispersal

Urticaceae began to diversify in Eurasia around the Late Cretaceous (68.7 Ma), with diversification perhaps accelerating around 45 Ma (Appendix S6). Remarkably, at least 92 LDD events were indicated, mostly out of Eurasia and most often to the adjacent regions of Africa and especially SE Asia. Incorporating paleogeographical evidence, at least 76 must have crossed at least one ocean (Appendix S6).

Potential for seed transoceanic LDD in Urticaceae

Migratory birds can be a major mechanism for transoceanic LDD (van der Pijl 1972; Heleno & Vargas 2015). Although most Urticaceae fruits are not edible, certain species' achenes (e.g. *Debregeasia longifolia*) are ingested by some small birds (Zeng-Yuan Wu, pers. obs.). Most birds do not retain seeds in their digestive tracts for long periods

(Proctor 1968) but small achenes could potentially make long journeys attached for example to mud on birds' feet (Cleland 1952), (Fig. 5, Table S15). Furthermore, occasional 'vagrant' birds blown off course by storms could aid dispersal in any direction. However, many Urticaceae live in wet forests, and birds that live there might be less likely to be blown off course than those frequenting open or coastal habitats. Likewise, seed from such habitats seem unlikely to be carried long distances by wind, as tree cover breaks up the flow of wind. Although some Urticaceae seeds have limited adaptation for wind dispersal (e.g. membranous achene wings; Kravtsova 2009) (Fig. 5), these tend only to be associated with short dispersal distances, rather than LDD (Higgins *et al.* 2003). Therefore, neither wind nor bird dispersal seems a likely mechanism for Urticaceae, though neither can be eliminated entirely (Table S15).

Floating vegetation islands provide a plausible dispersal mechanism for trees or epiphytes, and many account for some or all of three detected LDD events in *Procris*. An untested possibility is whether floating trees might also transport terrestrial forest species that are attached to soil around their roots (Fig. 5G). A robust test of whether epiphytes are favoured for LDD events requires examination of a family or clade with approximately equal numbers of epiphytic and terrestrial species.

Ocean current-mediated dispersal seems highly plausible within Urticaceae. Plant propagules can be carried long distances first by inland watercourses (Boedeltje *et al.* 2003), then later by ocean currents (e.g. Fig. 5F). We found no proof that growing near water increases the chance of LDD in Urticaceae, but seeds of species not growing close to water might still blow into streams regularly. One caveat to this is that in around half

the species examined, most or all seeds will sink and/or germinate in fresh water, within 15 to 80 days depending on the species, and hence could not conduct or survive a subsequent journey in seawater. Hence seawater dispersal will only work for those species if preceded by little or no time in fresh water; hence LDD is more likely if these grow relatively close to the coast. For others, notably *Maoutia puya* and *Oreocnide integrifolia*, seeds can remain buoyant and not germinate during long periods in fresh water, and likewise in seawater, suggesting that waterborne dispersal could work even from a starting point far inland.

For LDD by seawater to succeed, seed must both float and remain viable for long periods. Crucially, our data showed that all Urticaceae seeds examined are much less dense than water, with air-filled cavities, hairs and wings all sometimes contributing to buoyancy. Darwin (1856) observed that most kinds of seed sink, so Urticaceae might be better equipped for LDD over water than many other families. Most species examined exhibited little seed sinkage in salt water during 220 days, and what sinkage there was occurred mostly in the first 20 days, implying that after this buoyancy becomes stable, and could continue for a long time after 220 days. Only two of the 21 species tested, *Pellionia yunnanensis* and *Lecanthus peduncularis* looked as if seed sinkage will provide a significant obstacle to LDD in seawater. Seed that only partially sinks (i.e. is neutrally buoyant), can remain effectively suspended in the interior of the water column, where like floating seed they can still be moved and influenced by currents generated from tides, wind, waves, sea swell and hydrodynamics, as occurs for some seagrass seeds (McMahon *et al.* 2014). Even seed that has sunk can be moved

along the sediment surface by currents or wave driven oscillatory flows (McMahon *et al.* 2014), although this would not allow crossing of deep ocean.

Surface currents and winds provide passive transport for seeds drifting at sea (Hawlitschek *et al.* 2017), and the mean speed of ocean currents is 0.1-0.3 m/s (Nathan *et al.* 2008). Seeds of many Urticaceae remain viable following ten months' immersion in seawater, making possible a dispersal distance of at least 2592 km via ocean currents, close to the nearest distance between Africa and South America (~2800 km). Oceanographic current modeling also indicated that many of the detected LDD events could plausibly have occurred via ocean currents, before seed died or sank. Dispersal across oceans might also be aided by archipelagos such as Hawaii (Harbaugh *et al.* 2009), serving as dispersal "stepping stones", with our data suggesting at least one possible LDD event out of Hawaii (Appendix S5).

Therefore, similar with the propagules of marine species (Harwell & Orth 2002; Kennedy *et al.* 2016; Smith *et al.* 2018), viable seeds of Urticaceae could plausibly travel long distances via seawater. A further significant obstacle, however, may be the establishment stage.

Implications of ecological traits for LDD mechanisms in Urticaceae

For plants, LDD usually involves rare events driven by complex and highly stochastic processes (Nathan 2006). Following long journeys in seawater, seeds could be driven inland by extreme meteorological events such as stormy winds or floods, although more frequent events allow arrival in coastal areas or tidal floodplains (Fig.

5). Extreme events could also aid the incoming seed by disturbing the recipient habitat, reducing initial competition and favoring species adapted to disturbed environments. Consistent with this, those Urticaceae nodes undergoing LDD tended to occupy significantly more disturbed environments than did the family on average. Furthermore, at least seven Urticaceae genera contain species that occur in periodically disturbed littoral environments (Z.-Y. Wu, pers. obs.); such species could establish relatively easily following ocean seed dispersal. LDD might also favour species of disturbed habitats because these tend to be generalists, and hence more likely to establish in a novel environment; crucially this third argument applies to LDD via any method, whereas the first applies only to seawater dispersal, and the second to ocean dispersal in general. Hence the observed trend fits seawater dispersal well, but does not exclude other methods.

Seawater or wind dispersal both involve seeds travelling individually, introducing a major obstacle at the establishment stage, i.e. going from one individual to a population, unless the organism can self-fertilize. Conversely, birds or floating island dispersal could bring seeds in groups (Fig. 5, Table S15). Hence monoecious and self-compatible plants should be more likely to undergo LDD than dioecious or self-incompatible (SI) species (Baker 1955). However, 48.35% of detected LDD events involved dioecious taxa, compared to 54.98% of all nodes, so dioecy is not a major obstacle to LDD in Urticaceae. This weak effect can be explained if most monoecious Urticaceae are self-incompatible (data on SI in the family are lacking), meaning they too should require two seeds for establishment. Potentially, a dioecious species might

occasionally self via an occasional female flower on a male plant, or *vice versa* (Varga-
Frutis *et al.* 2014; Varga & Kytöviita 2016). Moreover, monoecy arose at least 84 times
during Urticaceae evolution (Fig. S4), often associated with transitions of habit and
disturbance, suggesting an ability to switch breeding strategy when circumstances
select for it. Both might be triggered by founder effects, aiding establishment.
Otherwise, two seeds are needed. In a habitat that undergoes regular disturbance and
inundation involving seawater, including tidal inland riversides, a second seed might
arrive within the lifespan of the original plant. Alternately, multiple seeds might arrive
and germinate simultaneously following a catastrophic event (Fig. 5, N, Q). Otherwise,
scraps of plant washed into the sea (“vegetable rubbish”; Darwin, 1856) might float
across the ocean, with multiple viable seeds contained in fruiting bodies (Fig. 5, E).
Nonetheless, for Urticaceae, establishment represents a significant obstacle to
successful LDD, probably second only to sea crossing itself. Much more data are
needed, especially on SI, in order to determine the most likely way that this obstacle
was overcome.

Furthermore, we inferred that the LDD events and all four tested traits were
phylogenetically conserved, therefore, LDD events in Urticaceae were strongly
associated with the evolution of conserved traits. The traits we assessed might
adequately represent LDD-linked traits, but there are almost certainly other traits we
did not include in our analyses that could also be informative regarding LDD events.
Of course any traits associated with LDD would not have actually been selected to
optimize LDD, since there would not have been any population-level advantage locally,

but nonetheless their evolution influenced which lineages successfully underwent LDD.

To the best of our knowledge, this is the first study to use multiple lines of evidence to examine seed transoceanic LDD in a widely distributed group that is not specialized for coastal habitats. Within Urticaceae, we inferred at least 76 LDD events that must have involved a journey over across oceanic waters, a result that emphasises the frequency and hence profound global importance of LDD for generating modern plant distributions. Seawater appears to provide the most feasible LDD medium, because seeds of many Urticaceae can float for long periods, and they remain viable after ten months in seawater. This permits very long distances to be covered by living and floating seeds, via ocean currents, and many species' seeds might live well beyond our 10-month test period. Furthermore, a bias towards disturbed habitats among dispersing lineages fits a hypothesis that seeds in seawater can come ashore onto viable ground that is disturbed, either periodically by tides, or dramatically by extreme events. Therefore, other than the ocean crossing itself, the biggest obstacle to LDD might be the establishment of breeding populations, at least for dioecious or self-incompatible taxa. Possible solutions to this include arrival of multiple seeds by various mechanisms (Fig. 5), or occasional sex switching that allows selfing. Given the long time-scales involved, the need for just one highly unlikely event is surmountable. Future work on breeding systems is needed to investigate this issue further. Our work adds to the growing body of evidence showing the importance and frequency of LDD, but moreover contributes towards addressing that most intractable question of LDD: how it happens.

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Figure legends

Figure 1. Global biogeographical patterns of Urticaceae inferred by Lagrange. Map shows the eight biogeographical regions in colors as defined in this study. Clades are marked by numbers in a black box. Circles with numbers indicate fossil calibration points. Pie charts above nodes show the biogeographical ancestral reconstruction results, with colors referring to the different regions as indicated in the map. Colored boxes behind tips indicate the distributions of species, as indicated in the map. Inferred dispersal events (D) are marked where appropriate on internal branches. (a) relationships between main clades; (b) biogeographical patterns of Clade I; (c) biogeographical patterns of Clade IV; (d) biogeographical patterns of Clade III; (e) biogeographical patterns of Clade II.

Figure 2. Effect of salinity (1, 3.5, 5 and 8% NaCl) and immersion time on the seed viability percentage (VP) of 12 species. a) *Debregeasia longifolia*, b) *Boehmeria penduliflora*, c) *Droguetia iners* subsp. *urticoides*, d) *Parietaria micrantha*, e) *Pilea pumila*, f) *Elatostema stewardii*, g) *Gonostegia hirta*, h) *Poikilospermum suaveolens*, i) *Laportea bulbifera*, j) *Dendrocnide basirotunda*, k) *Maoutia puya*, l) *Urtica dioica* subsp. *dioica*.

Figure 3. Percentage of floating seeds versus days in seawater for 21 selected species in our study.

Figure 4. Simulation of dispersal process for a seed released from the closest extant distribution point within the source clade, to a point within the range of the clade derived from an LDD event, assuming passive drifting via ocean currents. (a) *Debregeasia longifolia*, (b) *Laportea bulbifera*, (c) *Poikilospermum suaveolens*, (d) *Musanga cecropioides*, (e) *Droguetia iners* subsp. *urticoides*, (f) *Parietaria micrantha*, (g) *Pouzolzia elegans* var. *elegans*_Po11+Pipturus (Pip1+Pip7+Pip10), (h) *Neraudia*+sistergroup.

Figure 5. Plausible mechanisms for long-distance dispersal across an ocean barrier in Urticaceae. Colours indicate start (yellow), middle (orange) and end (red) of a journey via water. **A-D** = means of seeds reaching the sea: **A**, seeds or scrap of plant enter sea directly from land; **B**, same but begins by entering river then carried into sea by river;

C, growing on or around roots of large tree that falls into river and is carried to the sea,
 becoming floating vegetation island; **D**, same as C but plant begins as epiphyte. **E-H** =
 forms in which they cross the sea, in all cases propelled by ocean currents: **E**, seeds
 contained within scrap of floating plant; **F**, seeds (achenes in Urticaceae) float on their
 own; **G and H**, plants or roots or as epiphytes carried on floating tree, can be dead with
 seeds on them, or still alive. **I-J** = transport by air: **I**, blown by wind; **J**, carried by bird,
 mostly likely a vagrant blown off course. **K-Q** = methods of arrival on land from the
 sea. **K**, scrap of plant washed ashore, after which seeds might blow inland; **L**, floating
 seed washes ashore on beach or further inland if very high tide; **M**, carried ashore by
 animals that move between sea and land; **N**, seeds carried inland by tsunami; **O**, carried
 upriver (e.g. by tidal bore) and deposited on floodplain; **P**, floating vegetation island
 comes ashore and seeds can then blow inland; **Q**, seeds carried inland by tornado,
 waterspout or other extreme weather event. Where pairs of seeds are shown (**E**, **G**, **H**,
K, **P**) this indicates a mechanism with a high probability of transporting two seeds at
 once, overcoming potential barriers to establishment from self-incompatibility or
 dioecy.

Figure S1. Phylogenetic tree produced by Maximum Likelihood (ML) analysis based
 on data matrix with plastid, mitochondrial, and nuclear datasets combined. Clades are
 referred to by numbers in the box, numbers above branches (ML/MP/BI) are support
 scores from Maximum Likelihood (bootstrap), Maximum parsimony (bootstrap) and
 Bayesian posterior probability.

Figure S2. Global biogeographical patterns of Urticaceae inferred by S-DIVA. The map, clad names, circles with numbers, pie chart, and colored boxes behind tips exactly same as the scheme of Fig. 1. Inferred dispersal (D) is also marked where appropriate on internal branches.

Figure S3. The lineage through time plot (LTT) for Urticaceae. The solid line is derived from the maximum clade credibility tree, while the area shaded in grey represents the 95% confidence interval from the random 1000 trees of the BEAST analyses. The blue interval represents a period when Urticaceae underwent relatively rapid diversification.

Figure S4. Ancestral state reconstruction of four selected characters in Urticaceae. The clad names and plotted numbers exactly same as the scheme of Fig. 1. The character states at the Urticaceae node indicate the ancestral states of the family. State changes are indicated on the branches using same forms as nodes respectively.

Figure S5. (A) Seed germination of *Debregeasia longifolia* following immersion in 0% NaCl solution (distilled water) for 10 days. (B)-(D) Seed germination of *Gonostegia*, *Pilea*, and *Urtica* respectively, one week after being transferred to 1% water agarose substrate following 30 days' immersion in 1% NaCl solution. (E)-(H) Seed germination of *Droguetia* three weeks after being transferred to 1% water agarose substrate following 90 days' immersion in 1% (E), 3.5% (F), 5% (G) and 8% (H) NaCl solution. (I) Seed germination of *Gonostegia* two weeks after being transferred to 1% water

agarose substrate following 150 days' immersion in 3.5% NaCl solution. **(J-K)** Seed germination of *Pilea* (J) and *Maoutia* (K) two weeks after being transferred to 1% water agarose substrate following 150 days' immersion in 1% NaCl solution. **(L)** Seed germination of *Parietaria* two weeks after being transferred to 1% water agarose substrate following 150 days' immersion in 5% NaCl solution.

Figure S6. Photos of seeds of 12 species, following seed coat removal for Tetrazolium tests. **(A-B)** living (red) and dead (white) seeds of *Dendrocnide basirotunda* (A) and *Maoutia puya* (B). For all others, only live seed is shown: **(C)** *Elatostema stewardii*; **(D)** *Debregeasia longifolia*; **(E)** *Laportea bulbifera*; **(F)** *Urtica dioica* subsp; *dioica*; **(G)** *Parietaria micrantha*; **(H)** *Poikilospermum suaveolens*, **(I)** *Boehmeria penduliflora*; **(J)** *Pilea pumila*; **(K)** *Droguetia iners* subsp *urticoides*; **(L)** *Gonostegia hirta*.

Figure S7. Percentage of floating and germinated seeds versus days in distilled water. The X axis represents the soaking time (days), the Y-axis represents the floating/germination percentage of the seeds.

Figure S8. Seed X-ray images. **(a)** *Boehmeria nivea*. **(b)** *Boehmeria penduliflora*. **(c)** *Dendrocnide basirotunda*. **(d)** *Laportea bulbifera*. **(e)** *Pellionia yunnanensis*. **(f)** *Poikilospermum suaveolens*. **(g)** *Droguetia iners* subsp. *urticoides*. **(h)** *Gonostegia hirta*. **(i)** *Pilea pumila*. **(j)** *Maoutia puya*. **(k)** *Nanocnide lobata*. **(l)** *Girardinia diversifolia* subsp. *diversifolia*.

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748 **Figure S9.** Achene surface comparing no immersion (A) with eight months' immersion
749 into 3.5% NaCl solution (B), for the following species: **(1)** *Boehmeria penduliflora*, **(2)**
750 *Dendrocnide basirotunda*, **(3)** *Laportea bulbifera*, **(4)** *Parietaria micrantha*, **(5)** *Pilea*
751 *pumila*, **(6)** *Gonostegia hirta*, **(7)** *Droguetia iners* subsp. *urticoides*, **(8)** *Debregeasia*
752 *longifolia*, **(9)** *Maoutia puya*, **(10)** *Urtica dioica* subsp. *dioica*.

Table 1. Summary of all LDD events detected based on Lagrange analysis, incorporating ancestral states of four characters for correlative nodes.

Taxa/Clades		Geographic Disjunction (Lagrange)	Age of disjunction (Crown age) (Lagrange)	Sexual system	Epiphyticlife style	Habitat wetness	Habitat disturbance
	3F	A→B	40.8 (30.9-57.1)-30.0 (20.3-41.4)	diecious	non-epiphytic	dry	semi-disturbed
	<i>Discocnide mexicana_167A+Discocnide mexicana_Di6</i>	A→G	27.2 (14.7-40.9)-5.7(5.2-19.5)	diecious	non-epiphytic	dry	semi-disturbed
	<i>Dendrocnode excelsa_D10</i>	A→E	4.5 (0.6-9.1)-present	diecious	non-epiphytic	wet	semi-disturbed
	<i>Dendrocnode sinuata_D1</i>	A→D	0.2 (0-0.6)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Dendrocnode meyniana_D2</i>	A→D	0.2 (0-0.6)-present	diecious	non-epiphytic	wet	semi-disturbed
Clade III	<i>Dendrocnode_sp_W1</i>	A→D	8.6 (3.3-14.5)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Urtica ferox_Q10</i>	A→E	15.8 (10.9-21.5)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Urtica pilulifera_Q20</i>	A→B	26.2 (18.7-33.8)-present	monecious	non-epiphytic	dry	completely disturbed
	<i>U. sp_U18</i>	A→B	5.7 (2.3-9.5)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Urtica urens_U25+U. urens_U27+U. sp_U19</i>	A→E	5.5 (2.5-9.1)-2 (0.5-3.9)	diecious	non-epiphytic	dry	completely disturbed
	<i>Urtica mollis_Q16+U. aquatica_Q6</i>	A→G	4.1 (1.8-6.8)-1.5 (0.3-3.1)	diecious	non-epiphytic	wet	semi-disturbed

<i>Urtica andicola_Q5+U. leptophylla_Q13+U. macbridei_Q14+U. magellanica_Q15+U. peruviana_Q19_U. magellanica_U33</i>	A→G	7.0 (6.5-13.6)-6.4 (4.3-9.1)	diecious	non-epiphytic	wet	semi-disturbed
<i>Urtica echinata_U34</i>	A→G	2.4 (0.9-3.8)--present	diecious	non-epiphytic	wet	semi-disturbed
<i>Urtica dioica subsp. dioica_J10+U21</i>	A→B&F	2.4 (0.9-3.8)-2.0 (0.7-3.3)	diecious	non-epiphytic	wet	completely disturbed
<i>Urtica sp_U21</i>	A→G	1.0 (0.2-2.0)-present	monecious	non-epiphytic	dry	semi-disturbed
<i>Urtica trichantha_Q24+Urtica echinata_Q9</i>	A→G	8.6 (5.7-12.0) -6.7 (4.3-9.1)	diecious	non-epiphytic	wet	semi-disturbed
<i>Hesperocnide tenella_331A</i>	A→F	7.0 (4.3-9.1)-present	monecious	non-epiphytic	wet	semi-disturbed
<i>Utica_angustifolia_U1</i>	A→D	3.2 (2.8-7.1)-present	diecious	non-epiphytic	wet	semi-disturbed
<i>Touchardia latifolia_T1+Urera (Ur1+Ur2+Ur18+B30)</i>	B→H	12.8 (9.8-24.0)-10. (5.1-15.6)	diecious	non-epiphytic	dry	semi-disturbed
<i>Laportea_aestuans_L31+L30</i>	B→A& C& D& G	12.8-0.6 (0.03-1.46)	monecious	non-epiphytic	wet	semi-disturbed
<i>Laportea_bulbifera_L5</i>	A→D	3.4 (0.7-7.0)-present	monecious	non-epiphytic	dry	completely disturbed
<i>Laportea_mooreana_L12</i>	A→B	3.4 (0.7-7.0)-present	diecious	non-epiphytic	wet	semi-disturbed
<i>Laportea_alatipes_L10</i>	A→B	10.0 (3.2-18.2)-present	diecious	non-epiphytic	dry	semi-disturbed
<i>Urera nitida_Ur26+Urera sp._Ur25+Urera baccifera_Ur21+Urera baccifera_C4A</i>	B→G	17.3 (11.1-25.6)-6.7 (3.0-10.9)	diecious	non-epiphytic	dry	semi-disturbed
<i>Poikilospermum suaveolens_Pi3+Poikilospermum lanceolatum_Pi1+Poikilospermum_lanceolatum_Poi8</i>	B→A	17.3-4.1 (1.0-8.6)	diecious	non-epiphytic	dry	semi-disturbed
<i>Poikilospermum suaveolens_Pi3</i>	A→D	0.5 (0.04-1.2)-present	diecious	non-epiphytic	dry	semi-disturbed

Clade II	<i>Urera alceifolia_C11A+Urera lianoides_313A+Poikilospermum tangaum_Poi5+Urera caracasana_21+Urera caracasana_23561</i>	B→G	18.7 (11.1-27.6)-8.2 (3.5-13.4)	diecious	non-epiphytic	dry	semi-disturbed
	<i>Poikilospermum tangaum_Poi5</i>	G→D	4.7 (1.9-8.0)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Obetia pinnatifida_Ob1</i>	B→C	2.7 (0.5-5.6)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Obetia radula_Ob2</i>	B→C	4.6 (1.4-8.3)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Girardinia diversifolia_subsp_diversifolia_G9</i>	A→B& C& D	14.0 (4.8-25.0)-present	monecious	non-epiphytic	wet	completely disturbed
	<i>Girardinia diversifolia_subsp_triloba_G19+Girardinia _diversifolia_subsp_suborbiculate_G17</i>	A→B& C& D	14.0 (4.8-25.0)-4.5 (1.0-9.0)	monecious	non-epiphytic	wet	completely disturbed
	2A	A→G	51.6-28.8 (16.7-42.8)	diecious	non-epiphytic	dry	semi-disturbed
	<i>Pilea tetraphylla_P90</i>	A→B&C	16.3 (6.7-27.0)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Pilea (P101+P100)+Sarcopilea domingensis_302A</i>	A→G	18.2 (11.1-25.8)-14.5 (7.8-21.2)	diecious	non-epiphytic	wet	semi-disturbed
	<i>Pilea bemarivensis_P91+P92</i>	A→C	18.2 (11.1-25.8)-1.6 (0.3-3.5)	diecious	non-epiphytic	dry	semi-disturbed
	<i>Pilea microphylla_P100+P101</i>	G→A& B& C& D& E& F	14.5 (7.9-21.2)-5.9 (1.8-11.1)	monecious	non-epiphytic	wet	completely disturbed
	<i>Pilea peploides_var_major_P62</i>	A→D	4.1 (1.0-8.4)-present	monecious	non-epiphytic	wet	semi-disturbed
	<i>Pilea melastomoides_P20</i>	A→D	4.9 (2.3-7.8)-present	monecious	non-epiphytic	wet	semi-disturbed
	<i>Pilea pumila_P64</i>	A→F	24.5 (17.3-32.5)-present	monecious	non-epiphytic	dry	semi-disturbed

	<i>Procris (Pr2+Pr9+Pr10)</i>	A→D	25.5 (13.7-37.5)-13.6 (5.7-22.6)	monecious	epiphytic	wet	semi-disturbed
	<i>Procris_pedunculata_var_ornata_Pr10</i>	D→E	8.9 (2.8-16.1)-present	monecious	epiphytic	wet	semi-disturbed
	<i>Procris_crenata_Pr2</i>	D→A&B	13.6 (5.7-22.6)-present	monecious	epiphytic	wet	semi-disturbed
	<i>Lecanthus_peduncularis_Le1</i>	A→B&D	9.8 (2.5-18.9)-present	monecious	non-epiphytic	wet	semi-disturbed
	<i>1E</i>	A→G	40.5 (31.4-50.6)-27.1 (14.7-39.7)	monecious	non-epiphytic	wet	semi-disturbed
	<i>Boehmeria</i> (<i>B34+B37+B73+B36+B20+B39+B53+B88+B9+B47+B46+B24+B72+B47+B26+B1+B33+B16+B21+B40</i>)	G→A	17.8 (12.6-23.6)-12.3 (8.3-16.6)	monecious	non-epiphytic	wet	semi-disturbed
	<i>Boehmeria sp._Cy35</i>	A→G	2.0 (0.3-4.5)-present	monecious	non-epiphytic	dry	semi-disturbed
	<i>Boehmeria_densiflora_B53</i>	A→D	6.5 (4.0-9.3)-present	monecious	non-epiphytic	wet	completely disturbed
Clade I	<i>Boehmeria_macrophylla_var_macrophylla_B24</i>	A→D	5.9 (1.6-10.8)-present	monecious	non-epiphytic	wet	semi-disturbed
	<i>Boehmeria_macrophylla_var_scabrella_B26</i>	A→D	5.2 (2.5-8.3)-present	monecious	non-epiphytic	wet	semi-disturbed
	<i>Boehmeria_zollingeriana_var_blinii_B1</i>	A→D	4.6 (1.2-8.2)-present	monecious	non-epiphytic	wet	semi-disturbed
	<i>Boehmeria_clidemoides_var_diffusa_B16</i>	A→D	2.6 (0.7-4.9)-present	diecious	non-epiphytic	dry	completely disturbed
	<i>Boehmeria_cylindrica_20</i>	G→F	6.8 (2.1-12.0)-present	diecious	non-epiphytic	dry	semi-disturbed
	<i>Boehmeria_glomerulifera_B5</i>	A→D	2.0 (0.3-4.5)-present	monecious	non-epiphytic	dry	semi-disturbed

<i>Boehmeria nivea</i> _var_ <i>nivea</i> _B6+ <i>Boehmeria nivea</i> _var_ <i>tenacissima</i> _B32	A→B& C&D& E	1.26 (0.36-2.35)-0.5 (0.04-1.1)	monecious	non-epiphytic	wet	completely disturbed
<i>Sarcochlamys pulcherrima</i> _S1	A→D	1.3 (0.4-2.4)-present	diecious	non-epiphytic	dry	semi-disturbed
<i>Cypholophus</i>	G→D	13.2 (8.6-18.5)-9.9 (5.6-14.5)	monecious	non-epiphytic	dry	semi-disturbed
<i>Astrothalamus reticulatus</i> (As2+23592)	A→D	11.1 (5.5-17.5)-4.5 (1.4-8.0)	monecious	non-epiphytic	wet	semi-disturbed
<i>Debregeasia saeneb</i> _De17+De25	A→B	4.5 (2.1-7.2)-1.7 (0.4-3.5)	diecious	non-epiphytic	wet	completely disturbed
<i>Debregeasia longifolia</i> _De10	A→D	1.7 (0.3-3.5)-present	diecious	non-epiphytic	wet	completely disturbed
<i>Debregeasia squamata</i> _De5	A→D	3.1 (1.2-5.5)-present	monecious	non-epiphytic	wet	completely disturbed
<i>Neraudia</i> +its sistergroups	A→H	14.8 (9.0-21.2)-12.9 (7.9-18.2)	diecious	non-epiphytic	wet	semi-disturbed
<i>Pouzolzia poeppigiana</i> _Po10	H→G	9.0 (4.3-14.1)-present	monecious	non-epiphytic	dry	semi-disturbed
<i>Pouzolzia sanguinea</i> _var_ <i>sanguinea</i> _Po6+Po2	A→D	8.9 (4.0-14.1)-5.1 (1.4-9.4)	diecious	non-epiphytic	dry	semi-disturbed
<i>Pouzolzia zeylanica</i> _var_ <i>zeylanica</i> _Po7	A→B& D& E& F& G	4.1 (1.3-7.6)-present	diecious	non-epiphytic	wet	completely disturbed
<i>Gonostegia parvifolia</i> _Go1	A→D	4.2 (1.1-8.2)-present	monecious	non-epiphytic	dry	semi-disturbed
<i>Gonostegia hirta</i> _Go3	A→D& E	4.2 (1.1-8.2)-present	monecious	non-epiphytic	dry	completely disturbed
<i>Pouzolzia elegans</i> _var_ <i>elegans</i> _Po11	D→A	1.0 (0.1-2.7)-present	monecious	non-epiphytic	dry	semi-disturbed
<i>Pipturus arborescens</i> _Pip1+Pip7	D→A	1.0 (0.05-2.66)-0.4 (0.02-1.12)	diecious	non-epiphytic	dry	semi-disturbed

<i>Pouzolzia elegans</i> _var_ <i>elegans</i> _Po11+ <i>Pipturus</i> (<i>Pip1</i> + <i>Pip7</i> + <i>Pip10</i>)	H→D	4.8-2.9 (1.0-5.2)	monecious	non-epiphytic	dry	semi-disturbed
<i>Hemistylus macrostachya</i> _23597+ <i>Rousselia</i> <i>humulis</i> _23596	B→G	10.6 (5.2-16.0)-2.5 (0.2-5.7)	monecious	non-epiphytic	dry	semi-disturbed
<i>Hemistylus macrostachya</i> _23597+ <i>Rousselia</i> <i>humulis</i> _23596+ <i>Neodistemon indicum</i> (279A+Ne6)+ <i>Pouzolzia maxta</i> _288A	A→B	15.3 (9.7-21.2)-12.7 (7.3-18.2)	monecious	non-epiphytic	dry	semi-disturbed
<i>Neodistemon indicum</i> (279A+Ne6)	B→D	10.6 (5.2-16.0)-1.7 (0-4.9)	monecious	non-epiphytic	wet	semi-disturbed
<i>Pouzolzia maxta</i> _288A	B→C	12.7 (7.3-18.2)-present	monecious	non-epiphytic	dry	semi-disturbed
<i>Pouzolzia guineensis</i> _282A	A→B	12.3 (6.7-18.2)-present	monecious	non-epiphytic	dry	semi-disturbed
<i>Oreocnide trinervis</i> _O33	A→D	2.3-present	diecious	non-epiphytic	dry	undisturbed
<i>Oreocnide frutescens</i> _subsp_ <i>frutescens</i> _O2	A→D	1.8 (0.2-3.9)-present	diecious	non-epiphytic	dry	undisturbed
<i>Oreocnide rubescens</i> _O15	A→D	10.6 (4.9-17.4)-present	diecious	non-epiphytic	dry	undisturbed
<i>Didymodoxa caffra</i> _23599+its sister groups	A→B	30.7 (20.6-41.1) -24.3 (14.5-33.9)	monecious	non-epiphytic	dry	semi-disturbed
<i>Parietaria judaica</i> _11077+J7	A→B	10.4 (4.5-17.1)-2.4 (0.4-5.1)	monecious	non-epiphytic	dry	completely disturbed
<i>Forsskaolea angustifolia</i> _6515	A→B	17.1 (6.6-27.3)-present	monecious	non-epiphytic	dry	semi-disturbed
<i>Forsskaolea tenacissima</i> _F5	A→B	17.1 (6.6-27.3)-present	monecious	non-epiphytic	dry	semi-disturbed

	<i>Parietaria micrantha_Pa1</i>	A→B& E& G	(5.4-24.6) 14.7-present	monecious	non-epiphytic	dry	completely disturbed
	<i>Parietaria debilis_Pa5</i>	A→E& G	(5.4-24.6) 14.7-present	monecious	non-epiphytic	dry	completely disturbed
	<i>Drouguetia iners_subsp_urticoides_Dr1</i>	B→A& D	9.0 (4.0-14.5)-present	monecious	non-epiphytic	dry	semi-disturbed
	Clade 4A	A→G	44.1 (27.3-60.1)-19.6 (11.0-29.7)	diecious	non-epiphytic	dry	semi-disturbed
	<i>Musanga</i>	G→B	7.1-1.4 (0-4.3)	diecious	non-epiphytic	dry	semi-disturbed
	<i>Myrianthus</i>	G→B	5.7-present	diecious	non-epiphytic	dry	semi-disturbed
Clade IV	<i>Gibbsia insignis_Gi1</i>	A→D	10.4 (3.4-19.2)-present	monecious	non-epiphytic	dry	semi-disturbed
	<i>Maoutia setosa_M4+M2</i>	A→D	4.0 (0.7-8.8)-0.7 (0-2.2)	monecious	non-epiphytic	dry	semi-disturbed
	<i>Leucosyke quadrinervia_Leu4</i>	A→D	28.3 (14.7-43.0)-present	diecious	non-epiphytic	dry	semi-disturbed

#Note: Dates for LDD events are presented in the form (W-) X - Y (-Z), where X and Y are the nodes before and after the branch on which the event occurred, and W and Z are the older and younger HPD limits for X and Y respectively. Certain nodes lack HPD values due to weak phylogenetic support; age ranges for LDD events bounded by such nodes are given in the form X – Y, and stated to be approximate.









